NEUROPSYCHOLOGICAL AND NEUROIMAGING PERSPECTIVES ON CONCEPTUAL KNOWLEDGE: AN INTRODUCTION

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The modern era of study of the representation of object concepts in the human brain began in 1983 with a report by Warrington and McCarthy of a patient with preserved knowledge for animals, foods, and flowers, relative to inanimate objects (Warrington & McCarthy, 1983). This was followed the next year by a report of four patients with the opposite pattern of preserved and impaired category knowledge (Warrington & Shallice, 1984). Specifically, these patients presented with a relatively selective impairment for knowing about living things and foods. Since publication of these seminal case studies, over 100 patients have been reported with a category-specific deficit for biological categories (living things, especially four-legged animals), relative to inanimate objects (especially tools and other artifacts), and more than 25 cases with the opposite pattern of deficit (Figure 1). Heightened appreciation of the importance of these clinical cases for understanding the organisation of conceptual knowledge, as well as for object recognition, the organisation of the lexicon, and the storage of long-term memories, has also motivated an increasing number of functional brain-imaging studies of object category representation in the normal human brain. The goal of this special issue of *Cognitive Neuropsychology* is to provide a forum for new findings and critical, theoretical analyses of existing data from patient and functional brain-imaging studies.

THE THEORIES OF CONCEPT ORGANISATION

A number of different theoretical positions have been advanced to explain category-specific deficits. However, as described by Capitani, Laiacona, Mahon, and Caramazza (2003-this issue), much of the current debate centres on whether concepts are organised by property or by category.[1] Most investigators assume that the deficits are a direct consequence of the organisation of object properties in the brain. The best known property-based model of semantic category-specific deficits is the sensory/functional theory (S/FT), proposed by Warrington, Shallice, and McCarthy (Warrington & McCarthy, 1987; Warrington & Shallice, 1984).

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[1] Note, however, that the two types of organisation need not be mutually exclusive. It is possible that concepts are organised into domains and within domains the organisation may very well be by property type or correlation (Caramazza, 1998; see also Mahon & Caramazza, 2003-this issue).
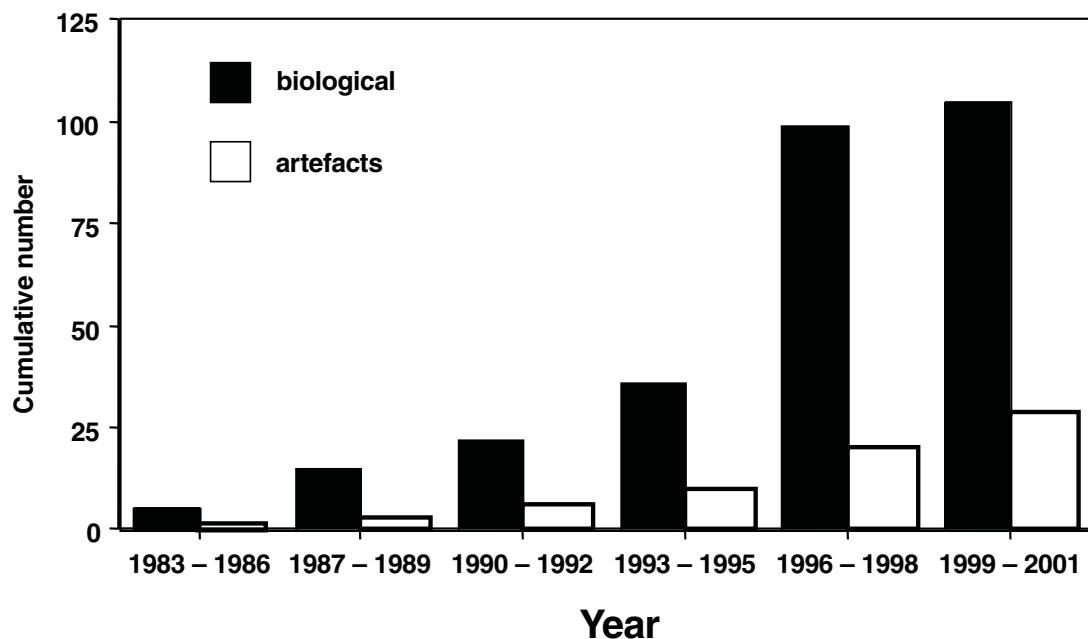

Figure 1. *Cumulative number of patients with category-specific disorders for biological objects and artefacts reported in the literature since 1983. Based on the review provided by Capitani et al. (2003–this issue).*

Although there are important differences among them, similar accounts have been proposed by a number of other investigators (e.g., Damasio, 1989; Humphreys & Forde, 2001; Martin, Ungerleider, & Haxby, 2000). The central idea behind S/FT-like theories is that conceptual knowledge about objects is organised by sensory features (e.g., form, motion, colour, smell, taste) and functional properties (the motor habits related to their use, typical location where they may be found, their social value, etc.).[2] Categories differ as to the importance or weight assigned to each of these properties. In this view, category-specific (C-S) semantic disor-ders occur when a lesion disrupts knowledge about a particular property or set of properties critical for defining that object category and for distinguishing among its members. Thus damage to regions where information about object form is stored will pro-duce a C-S disorder for animals. This is because visual appearance is assumed to be a critical prop-erty for defining animals, and because the distinc-tion between different animals is assumed to be heavily dependent on knowing about subtle differ-ences in their visual form (e.g., distinguishing among four-legged animals). A critical component of these models is that the lesion should affect

[2] Theories differ as to what is meant by "functional" properties. In the early literature, "functional" was used together with "associative" (functional-associative) to distinguish sensory from nonsensory properties of objects (e.g., Farah & McClelland, 1991). When used in the context of S/FT it has generally been interpreted in this sense. However, in some theories the term "functional" is restricted to the sense "use" and in others to the sense "motor habit." Sensory/motor theories of the representation of objects have tended to favour the latter sense (Martin et al., 2000). However, if we were to restrict "functional" to mean "motor habit" we would only be able to use the term "function" for a very small set of objects—primarily tools. This can be easily appreciated when we consider the functions of various artefacts. Thus, although some functions are associated with fairly specific motor patterns (e.g., scissors: used for cutting with a highly specific motor pattern), others are not associated with any specific motor pattern (e.g., car: used for transportation; house: used for shelter; shoes: used to protect feet; wedding ring: used to indicate a particular social status; etc.). These examples illustrate that "function" cannot be reduced to a specific sensorimotor system.

knowledge of all object categories with these characteristics, not only animals. In a similar fashion, damage to regions where information about how an object is used should produce a C-S disorder for tools, and all other categories of objects defined by the way in which they are manipulated.

Correlated structure accounts represent a related approach. These theories propose that the organisation of conceptual knowledge is dictated by the way in which properties of objects are statistically related to one another in the world, rather than by organisation of brain systems (for prominent examples of this approach, see Caramazza, Hillis, Rapp, & Romani, 1990; Devlin, Gonnerman, Andersen, & Seidenberg, 1998; Garrard, Lambon Ralph, Hodges, & Patterson, 2001; Tyler & Moss, 1997). S/FT-like models focus on constraints dictated by brain organisation, while correlated structure approaches focus on constraints determined by properties of the objects themselves. Nevertheless, both theories are property, rather than category, based.

The alternative to these property-based theories is the domain-specific theory (Caramazza & Shelton, 1998). On this account, our evolutionary history provides the major constraint on the organisation of conceptual knowledge in the brain. Specifically, the theory proposes that selection pressures have resulted in dedicated neural machinery for solving, quickly and efficiently, computationally complex survival problems. One implication of this theory is that the types of C-S disorders should be severely constrained. Likely candidate domains offered are animals, conspecifics, and plant life (and possibly tools). This account remains silent on the organisation of conceptual knowledge within domains; it could be organised either along the lines of correlated structure or sensory-motor theories, or of some other principle (see Mahon & Caramazza, 2003-this issue).

THE EVIDENCE FROM PATIENTS

The issue begins with an exhaustive review of the literature by Capitani and colleagues. Following a description of the theories along the lines set out above, the authors address two critical questions about C-S disorders. First, what are the categories of C-S disorders? Second, is there an association between the type of C-S deficit and type of conceptual knowledge deficit? For example, do patients with C-S deficits for animals have disproportionate difficulty retrieving sensory information? To answer these questions they offer a critical review of the "entire" published literature since Warrington and McCarthy's report in 1983. They conclude that two facts emerge from the review of the literature. One, the categories of C-S disorders are animate objects (animals), inanimate biological objects (fruits and vegetables), and artifacts. Thus, the authors argue that the categories of C-S disorders are more fine-grained than would be predicted by property-based models like S/FT, and are consistent with the predictions of the domain-specific account. Two, there is no association between type of C-S deficit and type of conceptual knowledge deficit. In fact, the authors show that knowledge of both sensory and functional information is equally impaired in the overwhelming majority of C-S cases. Thus, what the authors view as the central prediction of S/FT models, a relationship between type of C-S deficit and type of conceptual knowledge deficit, is simply untenable. These are strong claims. Yet the authors allow others to substantiate them by providing a description of the findings in each case study, including those that were deemed acceptable for their analysis, and those that were not. This description of behavioural performance, along with the information on lesion location, should prove useful for the field.

Evidence consistent and contrary to the claims of Capitani and colleagues is presented in the papers on patients with C-S disorders included in this Special Issue. Humphreys and Riddoch present a case series analysis of seven patients with C-S disorders for living things. The case-by-case analysis of individual patients on the same battery of tests provides a powerful means of testing specific hypotheses (a similar strategy is employed by Lambon Ralph, Patterson, Garrard, & Hodges, 2003-this issue; and Borgo & Shallice, 2003-this issue). One of the implications of the Capitani et

al. review is that C-S disorders of a particular type, say for animate objects, are relatively homogeneous disorders. In all patients, all types of knowledge about the impaired domain should be compromised, and the impairment should not be linked obligatorily with a selective impairment for a nonbiological category of objects (e.g., musical instruments). The patients studied by Humphreys and Riddoch (2003-this issue) suggest that the disorder may be more heterogeneous than the literature suggests. Although all of their patients showed an object naming deficit for living things, further testing revealed important differences. Moreover, these differences were related to differences in lesion location. As predicted by the domain-specific account, three of the seven cases had impaired knowledge for visual and functional information limited to living things. The others, however, had disproportionate difficulty with visual versus functional information. These latter patients also had particular difficulty with musical instruments. Humphreys and Riddoch interpret these and other aspects of the behaviour of their patients as posing difficulties for both the domain-specific and the standard form of S/FT. They go on to argue that the heterogeneous set of findings they report can be accommodated by the Hierarchical Interactive Theory (HIT; Humphreys & Forde, 2001).

The paper by Lambon Ralph and colleagues (2003-this issue) also offers data that are not easily accommodated by present views. Six patients with semantic dementia were evaluated. The logic here was to compare the performance of a single patient with a C-S disorder for living things with five other patients with a similar degree of semantic deficit as the target patient, but without a C-S disorder. As predicted by S/FT-type theories, the patient with a C-S disorder for living things had a greater impairment for sensory than functional information. However, contrary to S/FT, the other patients did as well. Thus, a greater difficulty for sensory than functional information is not causally related to C-S impairment for living things. The authors discuss how their cases present problems for all of the existing theories, and suggest that individual differences in the extent and quality of premorbid category knowledge may contribute to the observed variability in performance.

One of the key predictions of S/FT-like theories is that patients with C-S disorders for living things should also show a C-S deficit for other categories that are disproportionately dependent on sensory information. Borgo and Shallice (2003-this issue) provide a theory-driven approach to this question by testing a patient with a C-S disorder for living things on a set of "sensory-quality" categories. The logic here is that if a C-S disorder for living things is due to impaired knowledge of sensory properties, then the patient should also necessarily be impaired on categories defined primarily by sensory information (i.e., colour, texture). The categories assessed were edible substances (e.g., sauces, cheeses), drinks, and materials (e.g., metals, precious stones). As in the reports of Humphreys and Riddoch, and Lambon Ralph and colleagues, a multiple case-study approach is employed. The performance of a target patient with a C-S disorder for living things, MU, was contrasted to other patients matched with MU on performance with artefacts (see Borgo & Shallice, 2001, for a previous study of this patient). MU was impaired on the sensory-quality categories, and showed a much greater impairment for sensory than for functional properties for these categories. However, knowledge of both sensory and functional information was impaired for living things, but not artefacts. Moreover, the patients' pattern of performance on a property knowledge task differed depending on whether knowledge was probed using verification or production paradigms. Like the patients described by Lambon Ralph and colleagues, a greater deficit was found for sensory than functional information for all categories. Borgo and Shallice interpret their results as being consistent with the main predictions of S/FT. It is not clear, however, how the S/FT can account for MU's equal performance on probes of sensory and functional information for the category "living things." Furthermore, the reported association of a deficit for living things and sensory-quality categories is not a necessary one since Laiacona, Capitani, and Caramazza (in press) have reported a patient (EA) very similar to MU in all respects (including aetiology) except that he shows a dissociation

between poor performance for living things and spared knowledge for sensory-quality categories.

A central feature of S/FT-like models is that they predict that the deficit should generalise over categories that share a common sensory foundation, as exemplified by the patient described by Borgo and Shallice. In contrast, the domain-specific account predicts the existence of fine-grained category-specific deficits—in particular, that knowledge of fruits and vegetables can be dissociated from knowledge about animals. Although there have only been a few prior reports of such fine-grained dissociation, compelling evidence for the dissociation is presented in this issue for two new cases: one described by Crutch and Warrington (2003-this issue), the other by Samson and Pillon (2003-this issue). Both cases had a lesion of the left occipito-temporal cortex. The fact that these cases occur is problematic for the standard S/FT model, but Crutch and Warrington argue that the patient's behaviour can readily be accommodated by a multiple sensory and motor processing channel model along the lines initially proposed by Warrington and McCarthy (1987). On this view, the category fruit and vegetables can be dissociated from animals because colour and taste knowledge play a more important role for the former category than for animals. However, although knowledge of colour was not investigated in their patient, it was in the case studied by Samson and Pillon. Although this patient had impaired knowledge of many properties of fruits and vegetables, colour knowledge was intact (and see Miceli, Fouch, Capasso, Shelton, Tamaiuolo, & Caramazza, 2001, for a patient with the opposite dissociation). Clearly, the existence of these fine-grained C-S disorders is problematic for the standard form of S/FT, although perhaps less so for the multiple channel approach described by Crutch and Warrington. Nevertheless, there seems to be no principled reason why any property-based account would predict a C-S disorder for fruits and vegetables rather than any other object category. The fact that the domain-specific account does make this strong prediction needs to be addressed.

The domain-specific theory makes another strong prediction. Because domain-specific knowledge systems are innate, they should be present from birth and, if damaged, recovery of function should be minimal. Farah and Rabinowitz (2003-this issue) provide favourable evidence here for both these predictions. Their subject, Adam, sustained bilateral damage to occipitotemporal cortices at the age of 1 day. Tested at the age of 16 years, Adam showed a profound deficit for living but not for nonliving things (Adam also has a severe prosopagnosia, see Farah, Rabinowitz, Quinn, & Liu, 2000). Also consistent with the domain-specific account, retrieval of sensory and functional information were equally impaired for living, but spared for nonliving, things. Clearly, whatever was damaged at birth in this subject had profound implications for learning about certain categories of objects and not others. How best to characterise what was damaged is difficult to determine. Consistent with the domain-specific account, Farah and Rabinowitz suggest damage to a semantic category-specific component. Nevertheless, as the authors note, even in this case a property-based explanation cannot be ruled out.

All of these reports describe patients with C-S disorders for biological kinds. This bias in the frequency of C-S deficits for biological objects has been evident since the first reports by Warrington and colleagues (Figure 1). Nevertheless, a reasonably large number of patients with knowledge disorders effecting nonbiological categories have been reported. The contribution of Tranel, Kemmerer, Adolphs, Damasio, and Damasio (2003-this issue) focuses on the nonbiological category that has received the most attention; tools. The reason for this focus is self-evident. Tools are defined largely by their functional properties, which, in turn, are strongly correlated with shape. Moreover, these "functional" properties are clearly linked to sensory and motor systems involved in object manipulation and use. Thus, they are an ideal category for testing ideas about the functional neuroanatomy associated with the sensory and motor properties of objects. Tranel and colleagues tested a group of 90 subjects with unilateral lesions on two measures probing tool and action knowledge. Twenty-six subjects were identified who were impaired on one or both of the measures, and all but one patient showed intact knowledge of famous persons. Because this

was the only other category assessed, the selectivity of their deficit cannot be determined. However, unlike the reports discussed above, the goal of this study was not to explore the selectivity or nature of the deficit. Rather, the goal was to identify a group of patients with poor performance on the tool knowledge tasks in order to identify the locus of lesions.

The results of an analysis of lesion overlap were quite revealing. Three regions were identified, all lateralised to the left hemisphere. One included premotor and nearby prefrontal cortex, another involved parietal cortex, and the third was in the posterior part of the middle temporal gyrus. Each of these sites has, in turn, been linked to specific sensorimotor aspects of tool use. For example, single cell recording studies in monkeys have identified regions in ventral premotor and intraparietal cortices involved in grasping and manipulating objects. Cells in these regions also fire when monkeys see objects they have previously manipulated (see Jeannerod, 2001, for review). The site in the posterior part of the middle temporal gyrus was near, if not including, cortex involved in perceiving visual motion in monkeys and humans. Moreover, as will be discussed below, functional brain-imaging studies on tool representation have identified these same regions, and have also provided evidence for the functional properties of these regions along the lines discussed above. Thus, these findings provide evidence for a property-based network of regions in the human left hemisphere critical for knowing about tools.

The contribution by Mahon and Caramazza (2003-this issue), however, poses a serious challenge to this view. First, the authors clarify that the domain-specific account does not deny the possibility that one constraint on the organisation of conceptual knowledge in the brain is modality or type of information. However, the domain-specific theory does demand that the information within a modality- or property-specific semantic subsystem must be organised by category. According to the sensory/motor account (Martin et al., 2000), knowledge is stored in the sensory and motor systems active when information was acquired (in this case, information about tools). When this

system is damaged, knowledge about tools is impaired. Mahon and Caramazza reason that if the above statement were true, then it should not be possible to dissociate conceptual knowledge about an object from the ability to demonstrate and know about the use of that object. However, as they discuss, patients have been reported who indicate that these types of knowledge can be doubly dissociated. For example, patient WC (Buxbaum, Veramonti, & Schwartz, 2000), had a left parietal lesion and damage to sensorimotor representations, as evidenced by impaired knowledge of tool use, but intact knowledge of other aspects of tools (e.g., knowing that, for example, a radio and a phonograph have related functions, even though they are manipulated differently). Mahon and Caramazza argue that the existence of such cases makes the strong form of a sensory/motor property-based model untenable. Alternatively, however, one could argue from a sensory/motor perspective that patient WC's selective loss of knowledge about how objects are manipulated is because of damage to a region where this information, and only this type of information, is represented (i.e., motor sequences associated with an object's use). The best candidate regions would be left premotor and/or parietal cortices. In this way, one might be able to accommodate the dissociation of different types of conceptual knowledge about tools. However, this would entail abandoning the strong version of the theory, which holds that functional knowledge is directly represented in motor representations. Interestingly, Mahon and Caramazza also note that WC's modality-related dissociation between types of knowledge within a domain would be problematic for a domain-specific account that did not include a clear distinction between functional knowledge and the possible motor schemes for its realisation.

The patients discussed in these reports each pose challenges to the prevailing views on concept organisation in the brain. In their contribution, Simmons and Barsalou (2003-this issue) offer a new theoretical perspective. Their goal was to build on each of the three types of theories outlined above (S/FT-like, domain-specific, and correlated structure approaches), to form a theory that incorporates

the most important features of each position. The proposal also incorporates much of the thinking developed by Barsalou (1999) on how conceptual knowledge can be represented by perceptual symbol systems. Their proposal also draws heavily on Damasio's theory of convergence zones (Damasio, 1989; and see Crutch & Warrington, 2003-this issue, and Tranel et al., 2003-this issue, for other discussions of the role of convergence zones in the organisation of conceptual knowledge). Central to Simmons and Barsalou's model is the "similarity-in-topography principle", which proposes a mechanism to account for both property-level and category-level representations within a hierarchically organised system of convergence zones. Much like the HIT (Humphreys & Forde, 2001), this theory assumes a large number of principles in order to account for different patterns of C-S knowledge deficits (e.g., single category, multiple categories, disproportionate loss of sensory information, equal loss of sensory and functional knowledge) and lesion locations. One danger of these types of proposals, however, is that they may be so powerful that they can account for any pattern of impairment. To their credit, Simmons and Barsalou address this concern by providing specific predictions generated by their theory for both patterns of deficit and lesion locations. They also address differences between their proposal and related accounts (e.g., HIT).

FUNCTIONAL BRAIN-IMAGING STUDIES OF NORMAL INDIVIDUALS

To provide a context for the functional brain-imaging contributions, we first provide a brief review of findings from previous studies. For details, the interested reader can consult recent reviews by Bookheimer (2002); Josephs (2001); Martin (2001); Martin and Chao (2001); and Thompson-Schill (2002).

1. The brain regions most commonly associated with object category representation are ventral occipitotemporal, lateral temporal, posterior parietal (especially the intraparietal sulcus), and ventral premotor cortices.[3]

2. Activity within these regions is modulated by category. Objects belonging to different semantic categories produce different patterns of activity in these regions.

3. All objects tested to date show different patterns of activity in ventral occipito-temporal cortex. The most studied objects have been human faces, houses, animals, and tools. However, distinct object category-related patterns of activity have been reliably discriminated among relatively large sets of object categories (7 by Haxby, Gobbini, Furey, Ishai, Schouten, & Pietrini, 2001; 7 by Spiridon & Kanwisher, 2002; 10 by Cox & Savoy, 2002). Biological objects (faces, animals) typically show peak activity in the lateral portion of the fusiform gyrus, whereas the peak for artefacts (tools) is typically located in the medial portion of the fusiform. Ventral occipital regions (especially the inferior occipital gyrus) typically respond more strongly to biological objects (faces, animals) than to artefacts. However, activity associated with each object category is not confined to a specific location, but may cover a broad expanse of occipito-temporal cortex.

4. Each "category-specific" region in ventral temporal cortex (e.g., the fusiform face area) also responds, to a lesser extent, to other object categories. Controversy exists as to whether these smaller activations are nonspecific responses to the presence of a visual stimulus, or whether they are object category-related and thus of functional significance. At least some evidence favours the latter view (Chao, Weisberg, & Martin, 2002).

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[3] The claim that the regions identified are implicated in semantic representation of objects is not beyond criticism. Some of the regions may be involved in representing the structure of objects or the motor plans associated with the use of objects. Whether or not such information should be considered part of a semantic system or part of perceptual and motor systems is not resolved (for discussion, see Mahon & Caramazza, 2003-this issue)

5. In contrast to ventral cortex, lateral temporal cortex responds to a more limited number of object categories. The most common finding has been activation of the superior temporal sulcus (STS) in response to faces and animals (typically stronger in the right than the left hemisphere), and activation of the middle temporal gyrus in response to tools (MTG, typically stronger in the left than the right hemisphere). Objects shown moving in their characteristic fashion produce enhanced, category-related activity in this region. In contrast, category-related patterns in ventral cortex are relatively the same for static and moving images (Beauchamp, Lee, Haxby, & Martin, 2002).

6. Activation of the intraparietal and ventral premotor cortices has been strongest to tools and other manipulable objects. This activity is nearly always confined to the left hemisphere.

Much remains to be determined about the processing characteristics and/or type of information represented in these regions. Nevertheless, two conclusions may be drawn from these findings. First, the regions discussed above are involved in both perceiving and representing (storing) information about different object properties such as form (ventral occipito-temporal), motion (lateral temporal, with STS particularly responsive to biological motion, and MTG particularly responsive to tool-associated motion), and object use (intraparietal and ventral premotor regions). There are considerable data from monkey neurophysiology and lesion studies, as well as from human functional brain-imaging studies to support this view (for example, that STS is critical for detecting biological motion). Second, at least some of these purported object–property regions also appear to be organised by category. This seems most clear for posterior regions of the temporal cortex. In the fusiform gyrus animate objects produce more activity in the lateral fusiform than do manipulable artefacts, while the medial fusiform shows the opposite bias. In lateral temporal cortex, STS responds more to animate objects than to artefacts, while MTG responds more to manipulable artefacts than animate things.

With these findings in mind, we now turn to the neuroimaging papers. The section begins with a detailed analysis and review of the cognitive and associated anatomical components of a domain that has yet to be considered, the representation of number concepts. In their paper, Dehaene, Piazza, Pinel, and Cohen (2003-this issue) argue that number is a good candidate for a biologically determined semantic domain: Elementary number-processing ability has been documented in nonhuman primates without training, and in children prior to language development. In addition, as reviewed in their paper, functional brain-imaging studies and neuropsychological investigations suggest the existence of a distinct neural circuit for number processing. The authors propose that this circuit is composed of three separate regions in parietal cortex, each serving a specific function in the support of arithmetic operations. For our present discussion, the most interesting region is localised in the horizontal segment of the intraparietal sulcus (HIP). Dehaene and colleagues make a strong case that this region is essential for the semantic representation of numbers as quantities. One piece of evidence for this claim is that HIP is consistently more active for numbers relative to other object categories. In particular, HIP is more active when number names are contrasted to animal names, and when comparing numbers versus objects along a non-numerical scale (e.g., the ferocity of animals). As mentioned above, naming and making semantic judgements about tools also activates the intraparietal sulcus. This raises the intriguing possibility of a neural correspondence between the regions involved in representing properties associated with manipulating objects, and those involved in number representation. Although comparisons of locations of activity across tasks and laboratories must be made with caution, it may be noteworthy that the peak of activity, reported by Dehaene et al. across several studies, places the activity on the dorsal bank of the sulcus, while the peak activity reported across several studies of tools places the activity in a different location, deep within the sulcus (e.g., Beauchamp et al., 2002; Chao & Martin, 2000; Chao et al., 2002). Thus these regions may be anatomically distinct, but perhaps functionally linked.

Next follows a group of papers on the relationship between perceptual and conceptual processing. This issue is particularly relevant for functional brain imaging because it is often difficult to distinguish activity associated with perception of stimulus features from activity associated with higher-level visual and conceptual processes. In addition, the interaction between perceptual and conceptual processing is an important component of some formulations of property-based theories (e.g., Humphreys & Forde, 2001; Humphreys & Riddoch, 2003-this issue; Martin, 1998; Simmons & Barsalou, 2003-this issue). For example, in the HIT model (Humphreys & Forde, 2001), a lesion affecting the structural description system can produce a category-specific disorder for living things because of the overlap, or similarity, between the structural descriptions of items within this category (and see Humphreys & Riddoch, 2003-this issue). Because of the interactive nature of the system, a mild problem in accessing visual knowledge could result in a naming deficit for those categories that depend heavily on visual knowledge in order to distinguish among their members. On this view, a lesion to the structural description system should not lead to a deficit for artefacts. In contrast, the domain-specific account predicts that, just like conceptual knowledge, structural descriptions will be organised by domain (see Caramazza & Shelton, 1998). However, this theory makes no claims about the interaction between perceptual and conceptual processes.

The neuropsychological literature offers some, but not overwhelming, evidence for this interaction. One piece of evidence comes from patient ELM whose ability to learn new object–name paired-associates was influenced by the semantic relationship between the names paired with the objects. Semantically-related names resulted in poorer learning than semantically unrelated names (e.g., Arguin, Bub, & Dudek, 1996; but see comments on this and other putative cases of semantic agnosia by Capitani et al., 2003-this issue). There is also some evidence for perceptual/conceptual interactions in normal subjects. For example, repetition blindness (assumed to be a purely visual phenome-

non) can be influenced by semantic factors (Parasuraman & Martin, 2001), and performing an object decision task interferes more with retrieving words based on semantic (category fluency) than on spelling (letter fluency) constraints (a motor task produced the opposite pattern of interference; Martin, Wiggs, Lalonde, & Mack, 1994).

In their paper, Gauthier, James, Curby, and Tarr (2003-this issue) directly address this issue in normal individuals. Specifically, they ask whether performance on a visual task (in this case, object matching) can be influenced by conceptual knowledge. Using a procedure modelled after the studies carried out with ELM, they provide evidence that the ability to make a perceptual decision (visual matching of novel objects) is faster and more accurate when these objects were paired with semantically unrelated object names, or a dissimilar set of feature names, than when the names were from the same semantic category or when there was substantial feature overlap. One implication of these results is that they call into question our ability to firmly rule out conceptual influences on "perceptual" processes and perceptual impairments.

Neuroimaging evidence for a more intimate link between conceptual and perceptual processes is provided in the paper by Kan, Barsalou, Solomon, Minor, and Thompson-Schill (2003-this issue). Their primary goal was to obtain evidence consistent with the idea that conceptual knowledge is grounded in the perceptual system (see Barsalou, 1999). The study was motivated by previous reports of activation of a "visual area" (posterior region of the left fusiform) when generating mental images of objects (D'Esposito et al., 1997) and when answering questions about visual object properties (Thompson-Schill, Aguirre, D'Esposito, & Farah, 1999; but see comment by Caramazza, 1999). To test this idea, subjects performed a property-verification task. As predicted, activation was found in the left fusiform region, and this occurred only when the experimental design required subjects to retrieve semantic information to perform the property-verification task. The authors argue that the results provide additional evidence that conceptual knowledge is organised visually and grounded in perception.

Further evidence for the interaction of perceptual and conceptual processing comes from studies showing that animate objects (faces, animals) activate early visual processing areas (specifically, medial occipital cortex and the inferior occipital gyrus) to a greater extent than tools and other inanimate objects (e.g., houses). For example, relative to tools, enhanced occipital activity has been found for naming line drawings and photographs of animals (Chao, Haxby, & Martin, 1999; Damasio, Grabowski, Tranel, Hichwa, & Damasio, 1996; Martin, Wiggs, Ungerleider, & Haxby, 1996), naming silhouettes of animals (Martin et al., 1996), making same/different judgements with animal pictures (Perani et al., 1995, 1999), matching-to-sample, and simply viewing animal pictures (Chao et al., 1999). The paper by Tyler and colleagues (2003-this issue) adds to this growing list of reports. Positron emission tomography (PET) was used to record brain activity while subjects performed a semantic categorisation task with object pictures (animals, tools, vehicles, fruits and vegetables). The inferior occipital gyrus was found to be more active for animals than any of the other categories tested (the activity was reported to extend anteriorly into the right cerebellum; we return to this finding below). It was previously suggested (e.g., Martin et al., 1996, 2000) that greater activation of occipital cortex for naming animals than tools might reflect top-down activation of lower-level visual processing regions when detailed information is needed to distinguish between category members (e.g., to distinguish between different four-legged animals in order to name them), in much the same way that occipital cortex is activated during certain visual imagery tasks (Kosslyn et al., 1999; and see Hochstein & Ahissar, 2002, for a review of the role of top-down modulation in visual perception). Tyler and colleagues offer a similar explanation for their finding but attribute it to bottom-up visual processing of the stimuli. As they note, however, the enhanced occipital activity for semantic processing of the animal pictures was not due to visual complexity per se. Visual complexity failed to play a role in either the behavioural or imaging results in their study. Moreover, a bottom-up explanation is difficult to reconcile with findings of increased activation of inferior occipital cortex for animals relative to tools in studies that used written names, rather than pictures (Chao et al., 1999; Perani, Schnur, Tettamanti, Garno-Tempini, Cappa, & Fazio, 1999; and see Price, Noppeney, Phillips, & Devlin, 2003-this issue).

Aside from the occipital and cerebellar (but see below) findings for animals, no other category-related differences were found. However, this null finding is exactly what the authors predicted based on their conceptual structure model (Tyler & Moss, 1997, 2001). In their view, category-specific deficits emerge as a function of the content and structure of concepts within a non-differentiated distributed neural system. Within this system, category-specific deficits occur because some concepts are more protected from damage than others due to their structure. Living things have many shared properties that are highly intercorrelated (eyes, breathe), and fewer distinctive features, and these are weakly correlated with other properties of animals. In contrast, tools have the opposite arrangement of shared and distinctive properties. It is this disadvantage for distinctive relative to shared properties of living things compared to artefacts that results in the disproportionate number of patients with a deficit for living things. A direct prediction of this account is that there should be no category specificity in the normal brain (Tyler et al., 2003-this issue). Thus, support for an undifferentiated semantic system is dependent on showing that category-related differences in neural activity do not exist. This would seem to be a difficult position to defend given the neuropsychological and neuroimaging evidence reviewed thus far (and see previously cited reviews).

Tyler and colleagues (2003-this issue) do report two findings consistent with much of the functional imaging literature. First, performance on the semantic tasks was associated with activity in a widespread network including occipital, temporal, parietal, and frontal areas. Second, each of these areas responded to multiple object categories. However, in contrast to previous reports, no differences were observed between categories in any of the regions.

The authors pay particular attention to the fusiform gyrus because of prior reports that categories of living things, including human faces and animals, show enhanced activity in the more lateral portion of the fusiform, whereas tools show enhanced activity in the medial portion of the fusiform. These category-related activations are anatomically close and in fact, are overlapping (see Chao et al., 2002; Haxby et al., 2001; Haxby, Ishai, Chao, Ungerleider, & Martin, 2000; Martin & Chao, 2001; and Spiridon & Kanwisher, 2002, for evidence and discussion of these findings). Thus, one possibility for their failure to find differential activity is that PET lacks the spatial resolution to resolve distinct peaks of activation when they are generated from anatomically close sites. (For evidence that PET may fail to reveal category-related differences in the fusiform gyrus, whereas fMRI does reveal such differences, see discussion and Figure 6.4 in Martin, 2001.) This explanation, however, appears unlikely given that PET has revealed enhanced medial fusiform activity for naming tools versus naming animals (Whatmough, Chertkow, Murtha, & Hanratty, 2002), and greater activity in the lateral fusiform for animals relative to tools across a variety of semantic tasks (Price et al., 2003-this issue). Moreover, a lack of spatial resolution cannot explain a failure to find enhanced activity for tools in lateral temporal cortex, specifically the posterior region of the left middle temporal gyrus, as this has been reported multiple times using PET as well as fMRI (see above-cited reviews).

Tyler et al. (2003-this issue) used stringent criteria for the identification of category-specific regions. The area should respond more to one category versus the others combined, as well as more to that category versus each of the others separately. Nevertheless, even with these stringent criteria, activity specific for animals was found in the posterior region of the right hemisphere, extending anteriorly from the right inferior occipital cortex (as discussed above), to the right cerebellum. However, the location reported for this cerebellar activity was at 40–55–19 (standard coordinates measure in mm along three axes). This location is, in fact, essentially identical to the location Tyler and colleagues used as their target region for the lateral fusiform gyrus (39–54–17, based on Chao et al., 1999). Thus, one possibility is that the activity was not in the cerebellum (a unique finding for a region responding more to animals than other object categories), but rather was in the lateral fusiform gyrus. Greater activity in the lateral fusiform for animals relative to tools has been reported multiple times (including Price et al., 2003-this issue, at 40–54–14, which they label as the posterior region of the right lateral fusiform). In addition, this lateral portion of the fusiform is activated by faces (the so-called fusiform face area, FFA; along with the inferior occipital gyrus; see Haxby, Hoffman, & Gobini, 2000, for review). The coordinates for this face-responsive region are again nearly identical to those reported by Tyler and colleagues (40–55–19 reported as right cerebellum by Tyler et al., 2003-this issue, vs. the right FFA reported at 40–59–22 by McCarthy, Puce, Gore, & Allison, 1997; 39–59–16 by Haxby et al., 1999; 36–51–24 by Henson, Shallice, Gorno-Tempini, & Dolan, 2002; and 40–55–10 by Kanwisher, McDermott, & Chun, 1997, to cite a few locations from what is now a large and consistent literature). Thus, the activity reported by Tyler et al. may have been in the lateral portion of the right fusiform, not the cerebellum. If so, then their report may provide some of the strongest evidence for category selectivity in the lateral fusiform; in their study this area responded more strongly to animals vs. tools, animals vs. fruits, and animal vs. vehicles.

Of course, having established that a category of objects can differentially activate a region of the fusiform gyrus does not, in and of itself, tell us what the activation means. Price and colleagues (2003-this issue) directly address this critical question in this issue, and in so doing, return us to the thorny problem of the relationship between perceptual and conceptual processing. Based on previous findings by their group and others, the authors note that there may be an important distinction between activity in the posterior and anterior regions of the fusiform gyrus. Specifically, that posterior fusiform activity may be driven to a greater extent by visual features of the stimuli than by semantic variables, whereas activity in the anterior fusiform may be

more sensitive to semantic than visual variables. Evidence in support of this division of labour was obtained by a combined analysis of seven experiments in which subjects performed a variety of semantic tasks on natural kinds (including animals) and man-made objects (including tools), two experiments that required retrieval of semantic information about object-associated properties (colour, size), and one experiment on detection of simple features of meaningless visual stimuli—false fonts.

Consistent with previous findings, results of these analyses demonstrated an advantage for natural kinds (animals, fruits and vegetables) over man-made objects (tools, vehicles, and furniture) in the posterior region of both the left and right lateral fusiform gyrus. Moreover, both animals and fruits and vegetables showed more activity than tools. However, these category-related differences were found only for pictures of objects, not words. In addition, these posterior fusiform regions were activated by the feature detection task. Thus, the authors argue, the posterior fusiform may be a unimodal visual processing area. As a result, category-related differences may be driven bottom-up from visual input when the task requires increased structural differentiation (as emphasised by Humphreys and colleagues; see Humphreys & Riddoch, 2003-this issue). This could not, however, be due to the visual complexity of the objects because this region was strongly activated by fruits and vegetables, which have simple visual forms (see also Tyler et al., 2003-this issue). Price and colleagues also suggest that this unimodal region of the fusiform can be driven top-down depending on task demands. This proposal was supported by appeal to studies showing category-related differences in this region of the fusiform using mental imagery tasks (e.g., Ishai, Ungerleider, & Haxby, 2000) and word-processing tasks that required subjects to make decisions on the structural details of objects (e.g., Chao et al., 1999).

In contrast to these results, a more anterior region of the fusiform was activated only by the tasks requiring retrieval of visual information from object names. This area was strongly lateralised to the left hemisphere and did not overlap with the more posterior region where category-related differences were observed. Price and colleagues argue that this more anterior fusiform region may be a polymodal association area. Moreover, they suggest that visual information can be retrieved from this region without recourse to the more posterior category-sensitive regions. It should be kept in mind, however, that the information retrieval tasks focused on specific object properties, like colour, not on object categories per se. Nevertheless, as their report stresses, within a relatively circumscribed region (i.e., the left fusiform gyrus), there may be important differences in the processing characteristics mapped along a posterior-to-anterior gradient. As Price and colleagues note, these differences are consistent with anatomical and neurophysiological studies of monkey temporal cortex, and may help to explain some differences in patterns of performance in C-S patients (see Humphrey & Riddoch, 2003-this issue).

The final contribution to this issue, by Martin and Weisberg (2003-this issue), also offers data germane to the issue of the relationship between perceptual and conceptual processes and category-related activity in the fusiform gyrus and other brain regions. In contrast to the approach taken by Price and colleagues, in which differences between regions were based on how they were modulated by category and task demands, Martin and Weisberg took a different tack. Specifically, they sought to determine whether the pattern of category-related activity previously reported for living things (animals and faces) and artefacts could be found when the same visual objects were used to represent both categories. This would eliminate the concern that the category-related activity in posterior cortex was due completely, or in part, to bottom-up processing of visual differences in the shape or colour of the stimuli used to represent these categories.

To accomplish their goal, they developed a set of animations composed of simple geometric forms in motion. The study was modelled after the now classic demonstration by Heider and Simmel (1944), that simple geometric forms in motion can be interpreted, with little effort, as depicting animate beings with specific intentions. In their study, subjects were shown animated vignettes designed to

elicit concepts related to social interactions (e.g., children playing baseball, sharing ice-cream) or mechanical devices (a factory conveyor belt, a pinball machine). The results showed the same dissociation in ventral and lateral temporal cortices as seen for animate objects and artefacts. In ventral temporal cortex, vignettes interpreted as conveying social interactions elicited heightened activity in the lateral fusiform, while the mechanical vignettes led to heightened activity in the medial fusiform gyrus. In lateral temporal cortex, the social vignettes elicited bilateral activation of STS (stronger in the right than left hemisphere), as is typically seen with animate objects, whereas the mechanical vignettes showed activation in left MTG, as is typically seen for tools. The activity in the fusiform gyrus included both the posterior and anterior regions identified by Price and colleagues (2003-this issue). However, posterior and anterior sectors were not analysed separately. Nevertheless, these results can-not be due to bottom-up processing of the visual stimuli. The same geometric forms were used in both the social and mechanical animations. Thus, these category-related differences seem to reflect top-down influences.

In addition to these findings, Martin and Weisberg reported that the social vignettes activated a number of regions associated with social processing (for a recent review, see Adolphs, 2001). Specifically, stronger activity for social than mechanical vignettes was found in the anterior regions of STS, the amygdala, and in ventromedial prefrontal cortex. Activity in these areas was strongly lateralised to the right hemisphere. The sites associated with the social vignettes closely replicated and extended the findings reported by Castelli and colleagues using a different set of animations (Castelli, Happé, Frith, & Frith, 2000). By including the mechanical condition in the current study, Martin and Weisberg were able to distinguish between regions associated with processing within a specific conceptual domain (social, mechanical), from those involved in more general purpose, problem-solving aspects of the tasks. Within a property-based framework, the authors speculate that higher-order concepts such as "animacy" may be represented in a network of regions composed of areas that store knowledge of what animate objects look like (lateral fusiform gyrus), how they move (STS), coupled with areas for representing and modulating affect (amygdala and ventromedial frontal cortex).[4] It was also noted that a network dedicated to processing within the social domain is consistent with a domain-specific account. Specifically, it could be argued that selection pressures have equipped us with a dedicated neural system for quick and efficient problem solving within the social domain.

The functional imaging data seem to suggest that object concepts may be organised, in part, by property.[5] These data also seem to suggest that, within these regions, object concepts may be organised by category. This seems to be especially true of regions in posterior ventral and lateral temporal cortices. Thus one central question will be to determine how the cortex got this way. For domain-specific accounts, the answer is straightforward. An organisation by specific category types is a natural

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[4] This discussion overlooks some rather difficult issues. For example, the property "animate" is stated to be represented in a distributed network that includes information of various modalities, and therefore there is no need to postulate the existence of an independent, abstract representation "animate" in addition to the possible grounding of this property in a distributed network. But this seems unlikely to be correct. Consider the stimuli used by Martin and Weisberg. Animacy was inferred by the subjects from the pattern of movements of geometric shapes. This implies that "movement pattern" is sufficient to ascribe animacy to an object. Similarly, animacy may be assigned strictly on the basis of visual form without movement (a picture of a dog, say). But this means that no individual feature is necessary for the concept animate. Instead it seems that the property "animate" is triggered if any one of a set of specific properties (e.g., being capable of experiencing emotion) is present, implying a non correspondence between any one part and the whole concept. This implies, in turn, that "animate" is an abstraction from diverse patterns of features of different sorts—social, emotional, perceptual, and motor—and is not reducible to a sensory/motor pattern.

[5] It is important to highlight "in part" to stress that the concept of "dog" or "hammer" includes much more than sensory- and motor-related properties. We know a great deal about objects beyond what they look like, how they move, how they are used, how they feel, etc. Neuroimaging studies have, to date, revealed little if anything about where this other information is represented, even though most of our semantic memory must include this type of nonsensory/motor-based knowledge.

consequence, and the primary prediction of the theory. Property-based theories must impose additional constraints to explain how these category-related regions of activity emerge as a consequence of experience. Yet potential mechanisms are beginning to be identified that could account for the development of spatially organised clusters of neurons that respond to similar object properties (e.g., Erickson, Jagadeesh, & Desimone, 2000). This, and other potential mechanisms, may account for the development of an object category-like organisation in the brain.

FINAL COMMENTS AND FUTURE DIRECTIONS

We have discussed the papers in this Special Issue primarily in the terms used by the authors themselves. A major emphasis has been on whether the results support one or another theory of the organisation of conceptual knowledge in the brain. In this effort, we have presented the three major theories of the causes of category-specific deficits as if they constituted mutually exclusive proposals. However, a more accurate characterisation of the state of the art would be to argue that the three proposals actually represent three principles (domain, modality, property structure) about the organisation of conceptual knowledge that need not necessarily be mutually exclusive. That is, each theory can be seen as making assumptions at a different level in a hierarchy of questions about the organisation of conceptual knowledge (Caramazza & Mahon, 2003-this issue). At the broadest level is the question of whether or not domain-specific constraints play a role in the organisation of conceptual knowledge. Independently of the answer we give to this question, we would still need to answer the question of how concepts are represented and structured in the brain. The second question concerns whether conceptual representations are stored in separate modality-specific subsystems or a single amodal system. Thus, it is entirely possible that conceptual knowledge is organised by domains, and within domains by type of modality (see discussion in Mahon & Caramazza, 2003-this issue). Once

again, independently of how one answers the second-level question, we would still want to know how specific properties of objects are related to each other. Here, the focus would be on questions about how the distribution of the properties that characterise an object might shape the way individual property information is represented. Of course, it could turn out that some version of the correlated structure theory could account for all the facts from neuropsychology and neuroimaging without appealing to either domain-specific principles or modality-specific organisation. This outcome seems implausible given the evidence presented in this Special Issue. Alternatively, it could turn out that a new variant of the modality-based accounts would be able to explain all the data reviewed here. This outcome, too, seems implausible. Perhaps the time has come to consider how the three principles that underlie the different explanations of category-specific deficits might be integrated into a more comprehensive proposal. The combined consideration of neuropsychological and neuroimaging research is beginning to provide answers to these questions.

We believe that the papers included in this Special Issue of *Cognitive Neuropsychology* serve to highlight what we know (or think we know) and, more importantly, what we still need to know in order to begin to understand category-specific disorders and the representation of concepts in the human brain. Here we mention a few of these goals. First, much of the debate about the patients relies on their ability to retrieve information about sensory and functional object properties. To fully understand these patterns of deficit will require a much finer-grained analysis of these properties (see for example Cree & McRae, in press). Second, studies of patients who sustained damage very early in life (see Farah & Rabinowitz, 2003-this issue), and studies of patients with developmental disorders limited to a single domain (e.g., developmental prosopagnosia; De Haan, & Campbell, 1991) should be helpful in characterizing the nature of innate mechanisms. Third, the relationship between neuroanatomy and category-specific disorders is poorly understood and the functional imaging data have done little to clarify this issue.

Some of the imaging data fit well with the lesion data; especially with regard to knowledge of tools and other manipulable objects (see Gainotti, 2000; Tranel, Damasio, & Damasio, 1997; and Tranel et al., 2003-this issue). In contrast, the relevance of the complex organisation in ventral temporal cortex to category-specific disorders is unknown. Given the complex organisation of overlapping representations in this region revealed by fMRI, it seems highly unlikely that a lesion could selectively carve out one category-responsive region from another. This suggests that some of the critical regions for producing category-specific disorders, especially for living things, reside elsewhere in the brain. Detailed neuropsychological investigations of individual patients coupled with neuroimaging should help to clarify this issue (e.g., Mummery, Patterson, Wise, Vandenberghe, Price, & Hodges, 1999).

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